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# **Importance of dispersal routes that minimize open-ocean movement to the genetic structure of island populations**

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## **Abstract**

Islands present a unique scenario in conservation biology, offering refuge yet imposing limitations on insular populations. The Kimberley region of northwestern Australia has more than 2500 islands that have recently come into focus as substantial conservation resources. It is therefore of great interest for managers to understand the driving forces of genetic structure of species within these island archipelagos. We used the ubiquitous bar-shouldered skink (*Ctenotus inornatus*) as a model species to represent the influence of landscape factors on genetic structure across the Kimberley islands. On 41 islands and 4 mainland locations in a remote area of Australia, we genotyped individuals across 18 nuclear (microsatellite) markers. Measures of genetic differentiation and diversity were used in two complementary analyses. We used circuit theory and Mantel tests to examine the influence of the landscape matrix on population connectivity and linear regression and model selection based on Akaike's information criterion to investigate landscape controls on genetic diversity. Genetic differentiation between islands was best predicted with circuit-theory models that accounted for the large difference in resistance to dispersal between land and ocean. In contrast, straight-line distances were unrelated to either resistance distances or genetic differentiation. Instead, connectivity was determined by island-hopping routes that allow organisms to minimize the distance of difficult ocean

passages. Island populations of *C. inornatus* retained varying degrees of genetic diversity ( $N_A = 1.83 - 7.39$ ), but it was greatest on islands closer to the mainland, in terms of resistance-distance units. In contrast, genetic diversity was unrelated to island size. Our results highlight the potential for islands to contribute to both theoretical and applied conservation, provide strong evidence of the driving forces of population structure within undisturbed landscapes, and identify the islands most valuable for conservation based on their contributions to gene flow and genetic

**Keywords:** bar-shouldered skink (*Ctenotus inornatus*); CIRCUITSCAPE program; connectivity; genetic drift; island biogeography; isolation by resistance; landscape genetics; aislamiento por resistencia; biogeografía de islas; conectividad; deriva génica; genética de paisajes; programa CIRCUITSCAPE; *Ctenotus inornatus*

La Importancia de las Rutas de Dispersión que Minimizan el Movimiento en Mar Abierto de la Estructura Genética de las Poblaciones Insulares

### **Resumen**

Las islas presentan un escenario único para la biología de la conservación ya que ofrecen refugio pero a la vez imponen limitaciones sobre las poblaciones insulares. La región Kimberley del noroeste de Australia tiene más de 2500 islas que recientemente han llamado la atención como recursos sustanciales para la conservación. Por esto es de gran interés para los manejadores el entender las fuerzas conductoras de la estructura genética de las especies en estos archipiélagos. Usamos a la especie ubicua *Ctenotus inornatus* como modelo para representar la influencia de los factores del paisaje sobre la estructura genética a lo largo de las islas Kimberley. En 41 islas y en cuatro localidades continentales de un área remota de Australia, identificamos el genotipo de los individuos mediante 18 marcadores nucleares (microsatélites). Se utilizaron las medidas de diferenciación genética y diversidad en dos análisis complementarios. Usamos la teoría de circuitos y la prueba de Mantel para examinar la influencia de la matriz de paisajes sobre la conectividad poblacional y la regresión lineal y la selección de modelos con base en el criterio de información de Akaike para

investigar los controles de paisaje sobre la diversidad genética. La diferenciación genética entre las islas se pronosticó de mejor manera con los modelos de la teoría de circuitos que tomaban en cuenta la gran diferencia en la resistencia a la dispersión entre el océano y el suelo. En contraste, las distancias en línea recta no se relacionaron con las distancias de resistencia ni con la diferenciación genética. En cambio, la conectividad estuvo determinada por las rutas de salto de islas que permiten que los organismos minimicen la distancia de los pasos oceánicos complicados. Las poblaciones insulares de *C. inornatus* mantuvieron diferentes grados de diversidad genética ( $N_A = 1.83 - 7.39$ ), pero esta fue mayor en las islas cercanas al continente, en términos de unidades de resistencia-distancia. Como contraste, la diversidad genética no estuvo relacionada con el tamaño de la isla. Nuestros resultados resaltan el potencial de las islas para contribuir a la conservación teórica y aplicada, proporcionar evidencias sólidas de las fuerzas conductoras de la estructura poblacional dentro de un paisaje no perturbado, e identificar a las islas más valiosas para la conservación con base en sus contribuciones al flujo génico y a la diversidad genética.

## **Introduction**

Landscape genetics has evolved over the past decade into an innovative and important tool for conservation (Eldridge et al. 2004; Manel & Holderegger 2013; Bolliger et al. 2014). Decreased genetic diversity may reduce a population's ability to survive demographic or environmental stochasticity because the effects of genetic drift are increased and may overwhelm the effects of natural selection (Hutchison & Templeton 1999; Lindenmayer & Fischer 2007; McCarthy et al. 2011). It is therefore important to understand the ways in which landscape characteristics such as amount of habitat, connectivity of habitat patches, and the composition and permeability of the landscape matrix influence genetic structure within and between populations (Hoeck et al. 2010).

Island systems present a unique opportunity to study the influence of habitat size and isolation on population structure (Wang et al. 2014). Insular populations are generally more discrete than those in habitat fragments on the mainland because water provides a near-complete barrier to dispersal for

many terrestrial species (Jordan & Snell 2008) and is a more uniform hostile matrix than the areas surrounding terrestrial habitat islands (e.g., Kupfer et al. 2006). Thus, island populations more closely resemble models used in population biology (White & Searle 2007).

In a meta-analysis of population size and genetic variation within wildlife populations, Frankham (1996) found a significant positive correlation between island size and levels of genetic variation. Additionally, there is empirical evidence that large islands with larger populations maintain higher levels of genetic diversity than their smaller counterparts (White & Searle 2007; Hoeck et al. 2010; Wang et al. 2014). When levels of genetic variation within island populations differ from what would be expected from island size alone, variation may also be explained in part by the level of geographic isolation, which governs the exchange of alleles between populations (Wilson et al. 2009). Mainland populations subjected to habitat loss and fragmentation face similar genetic consequences (Couvét 2002).

Many studies in which these effects have been examined were limited by the number of islands available (or sampled) in a particular region; interpretations are often based on fewer than 15 islands (Supporting Information). This may limit the confidence by which this information can be applied to conservation issues and may preclude the detection of patterns and processes operating on broader scales. The literature is consequently lacking examinations of larger systems that could confirm theories of island biogeography (MacArthur & Wilson 1967) and SLOSS (effectiveness of single large versus several small protected areas [Diamond 1975]), of which islands are held to be definitive exemplars.

Lizards are an attractive group for island studies due to their intermediate dispersal abilities over seawater relative to other groups such as birds or amphibians (e.g., Dobrovolski et al. 2012) and because they are relatively easy to sample. Patterns of genetic diversity in many herpetological studies examining continental island systems suggest that gene flow is limited between islands and therefore divergence of neutral markers is mostly driven by genetic drift (MacAvoy et al. 2007; Jordan & Snell 2008; Hurston et al. 2009). However, both anecdotal and direct evidence suggests that some lizards can move between islands actively (Southwood & Avens 2010) or passively on rafts or other

floating material (Censky et al. 1998). *Ctenotus* species are the most diverse genus of Australian lizards and are abundant throughout most of Australia (Cogger 2014). Consequently, they have been used as model species for a number of purposes in ecological and molecular studies (Rabosky et al. 2007).

The Kimberley region in Western Australia has been largely spared from much of the anthropogenic disturbance threatening Australia's northern vertebrate biota (Woinarski 1992). There are approximately 2633 continental islands of varying size and distance from the mainland along the Kimberley coast, most of which have been isolated from the mainland for approximately 8,000-10,000 years as a result of rising sea levels following the last Pleistocene glacial maximum (How et al. 2009). The most abundant and widespread vertebrate taxon throughout the Kimberley islands is the bar-shouldered skink, *C. inornatus* (Palmer et al. 2013), a habitat generalist distributed across subhumid and semiarid northern Australia (Maryan & Shea 2010). Little is known of its natural history, but closely related species (*Ctenotus saxatilis* and *Ctenotus robustus*) reproduce in the mid-late dry season (James & Shine 1985). Like other *Ctenotus*, *C. inornatus* is oviparous and most likely to produce one clutch per season.

The Kimberley islands provide an opportunity to examine a much larger and more complex island system than is often available. Studying their insular populations will provide insight into the factors driving population structure in this landscape. We examined the effects of island size and isolation on the genetic population structure of *C. inornatus* on 41 island and 4 mainland populations in the Kimberley region. The ubiquity of *C. inornatus* makes the species a particularly informative model to examine the effects of insularity on a terrestrial vertebrate species without the confounding elements of endangerment or rarity. We used microsatellite loci to measure levels of genetic diversity and differentiation within and between populations to determine the most appropriate measure of isolation in island systems and to demonstrate how habitat size and isolation influence genetic diversity within populations. In other words, we asked, is genetic structure determined by straight-line dispersal routes between islands, island-hopping connections (i.e., routes between a source island or mainland and destination island pieced together from short island-to-island connections to minimize ocean

crossings), or a legacy of historical connections prior to sea level rise? We also compared our findings, from an unusually large sampling effort, with the current theories of island biogeography and, based on our results, considered how islands can contribute to the conservation of vertebrate fauna.

## **Methods**

### **Sample Collection**

Sampling was carried out using a variety of capture techniques, including the use of box-traps, funnel traps, and active searching. The majority of tissue was collected by taking tips from lizard tails. However, when voucher specimens were collected, lizards were euthanized before the liver was taken for storage in 100% ethanol. All collecting and trapping was carried out in compliance with Western Australian Government Standard Operating Procedures in relation to the ethical use of wildlife. The Western Australian Museum worked under CALM permit SF004816 to collect fauna and a Department of Parks and Wildlife License to Use Animals for Scientific Purposes U18/2005.

### **Site Selection**

We selected for analysis sampled islands that encompassed a range of island sizes, distance from the mainland, and distance from other sampled islands (Fig. 1 & Supporting Information). Geographic distances (determined in ArcGIS version 10) were estimated between islands and the nearest neighboring island, between islands and the mainland, and between islands and the nearest river mouth, an expected source of rafting *C. inornatus* individuals. Island boundaries were derived from the GEODATA Coast data set (Geoscience Australia 2004). Measurements for the first 2 distance variables were based on the shortest straight-line distance between them (coastline to coastline). Distance to nearest river mouth included both the straight-line distance and a linkage-distance measurement that followed a stepping stone passage through islands. Linkage distance routes were delineated manually.

## **Microsatellite Amplification and Analysis**

We genotyped 425 individuals from 41 islands and four mainland sites at 18 microsatellite loci following protocols in Harradine et al. (2013). The number of effective alleles ( $N_e$ ) and observed ( $H_o$ ) and expected heterozygosity (unbiased;  $H_e$ ) were calculated for each sampling location in GenAIEx version 6.5b (Peakall & Smouse 2006) (Supporting information). We chose  $N_e$  and  $H_e$  to represent genetic diversity within populations because  $H_e$  corrects for small sample size and because  $N_e$  allows comparison of populations that have different numbers and distributions of alleles. Estimates of genetic differentiation between populations were calculated in GenAIEx with  $F_{ST}$  (estimated by  $\theta$ ) (Weir & Cockerham 1984) and  $R_{ST}$ .

## **Hypotheses of Patterns of Genetic Differentiation**

We used  $F_{ST}$  and  $R_{ST}$  values and Mantel tests (R package VEGAN) (Dixon 2003) to examine three hypotheses of the mechanisms driving spatial patterns of genetic differentiation. Under circumstances of equilibrium between gene flow and genetic drift, a pattern of isolation by distance is expected whereby genetic differentiation increases with geographical distance (Hutchison & Templeton 1999). Absence of this relationship suggests a dominant effect of genetic drift. Alternatively, an absence of isolation by distance may occur if geographic distance is not an appropriate measure of connectivity between populations. Our three hypotheses reflect different means of estimating the effective distance between populations and thus test the influence of different mechanisms that might drive connectivity across this island system.

### **HYPOTHESIS 1**

Organisms follow routes similar to a straight-line path, and ease of movement is uniform across the landscape. This straight-line connections hypothesis tests the traditional isolation-by-distance model; geographic distance between islands is the distance measure. Hypothesis 1 may be realistic for remote isolated islands. The remaining 2 hypotheses were investigated using circuit theory (McRae & Beier 2007) to remove both of the restrictions of the straight-line connections hypothesis. Effective distances between islands were modeled as a function of spatial variation in resistance to dispersal,



which informs both the routes traveled and the estimated effective distance between populations. Circuit theory models of connectivity recognize that organisms follow multiple pathways across a landscape and that detours from the shortest route, in geographic terms, may be easier to travel and have greater connectivity value.

## **HYPOTHESIS 2**

Ocean presents greater resistance to movement by terrestrial organisms than land and organisms use island-hopping connections. This hypothesis tests the isolation-by-resistance model. The mainland and islands were assigned resistance values of 1. Two values of ocean resistance were evaluated (10 or 100) to determine the relative strength of the barrier imposed by the ocean. Resistance distances in this model reflected the effect of island neighborhoods and the ability for organisms to follow island-hopping routes that reduce cumulative dispersal resistance relative to shorter straight-line routes requiring longer ocean passages.

## **HYPOTHESIS 3**

Observed genetic relationships are a legacy of historic patterns when all islands were connected to the mainland and populations become progressively isolated from each other by sea level rise. The resistance surface in this historical connections hypothesis has greater spatial nuance than the binary ocean versus land resistance surface used in hypothesis 2. Specifically, resistance is a function of ocean depth (isolation by bathymetry). We assigned the mainland and islands resistance values of 1 and ocean pixels a resistance value equal to the sea depth (data source: Whiteway 2009) plus 10 (thus, resistance for each ocean cell was  $\geq 11$ ). Under hypothesis 3, genetic relatedness is an effect of the differential time of isolation and age of last land connection between island pairs, as proxied by the bathymetry.

## **Circuitscape Models of Connectivity**

Circuitscape (McRae & Beier 2007) was used to compute pairwise resistance distances between analyzed populations. Circuitscape represents the landscape as an electrical circuit, where each cell in the raster grid is a unique resistor connected to eight surrounding cells. Resistance distances are the

effective resistance between pairs of populations. They integrate over all possible routes through the landscape and are calculated by setting the location of one population as the current source and the other as the ground. All Circuitscape analyses were conducted at the 0.0025 dd resolution of the bathymetry data. The resulting pairwise resistance matrix was then correlated with the previously described genetic differentiation matrix with a Mantel test. Because a parallel investigation (Harradine et al. 2015) found that the genetic structure of these populations was spatially autocorrelated within 50 km separation distances, all Mantel tests were conducted on both the full matrices of all island pairs and on reduced matrices of only island pairs separated by 50 km or less. We compared competing hypotheses with a partial Mantel test (implemented in the VEGAN package; see Supporting Information) because the model with the best support should show a significant positive partial correlation with genetic distance after controlling for each of the competing models (McRae & Beier 2007).

Once identified, we used the best resistance surface to estimate resistance distances between each island and the mainland for inclusion in further analyses (below) and to produce a map of net current density. These Circuitscape runs considered only the mainland as the current source, but they iteratively treated each island as the ground. A map of net current density was produced to illustrate the current from the mainland that passes through each cell, given the resistance landscape, which represents the expected flow of individuals traversing a given location and provides a measure of the importance of each island to landscape connectivity.

### **Patterns of Genetic Variation on Islands**

We tested effects of island characteristics on genetic variation ( $N_e$  and  $H_e$ ) within island populations with multiple linear regression and model selection using Akaike's information criterion (AIC; Quinn & Keough 2002) in R (R Core Team 2012). The AIC is a measure of goodness of fit and model complexity, whereby the best (lowest) score is given to the model that provides the maximum fit for the fewest predictors (Quinn & Keough 2002; Zuur et al. 2009). Explanatory variables included island size, distance between island and mainland (both geographic distance and the optimized resistance

distance), distance to nearest island, and distance to the nearest river mouth or outflow (both shortest distance and linkage distance).

Preliminary data exploration identified outliers for island size and distance to nearest island. To reduce the influence of outliers, size and distance to nearest island were log transformed. The residuals values were assessed to ensure that model assumptions were not violated. We assessed the models using a best subset process (Quinn & Keough 2002), whereby 15 models were created using all available subsets of explanatory variables, including a global model with all explanatory variables. This was repeated for both of the response variables (Supporting Information). The best model for each response variable was then selected using AIC corrected for small sample size (AICc) (Burnham & Anderson 2002) in R package AICcmodavg (Mazerolle 2006). The relative importance of each explanatory variable was assessed by summing the AIC weights over all models in which a given variable was used.

## Results

### Contribution of Isolation by Distance, Barriers, and Bathymetry to Differentiation

Mantel test analyses of  $F_{ST}$  and  $R_{ST}$  led to similar conclusions; thus, only the results of models of  $F_{ST}$  are presented here. Hypothesis 1 (straight-line connections) received little support. Differentiation between the sampled populations showed no pattern of isolation by distance based on geographical distance (Fig. 2a) ( $r = 0.06$ ,  $p = 0.234$ ). When restricting our analyses of the geographic structuring of genetic differentiation to island pairs within 50 km of each other, a weak isolation-by-distance pattern was observed ( $r = 0.31$ ,  $p < 0.001$ ). However, the best model for genetic differentiation was the island-hopping connections (hypothesis 2) model. It accounted for the influence of ocean as a barrier to dispersal and connectivity mediated by the effectiveness of island-hopping routes between populations (Fig. 2b) ( $r = 0.69$ ,  $p < 0.001$ ). There was little difference between the model that assigned a resistance value of 100 to water and the model that assigned a resistance value of 10 to water. Results shown are for the former. The historical connections model

(hypothesis 3) showed a weaker yet still significant correlation with  $F_{ST}$  (Fig. 2c) ( $r = 0.50, p < 0.001$ ). Contrary to the tests of isolation by distance, isolation by resistance and isolation by bathymetry models were stronger when evaluating all island pairs than when limiting tests to 50-km genetic

In partial Mantel tests evaluating the strength of support for competing hypotheses, hypothesis 2 lost little explanatory power when partitioning out the effects of hypothesis 3 ( $r_{\text{partial}} = 0.55, p < 0.001$ ). In contrast, no explanatory power of hypothesis 3 remained after partitioning out hypothesis 2 ( $r_{\text{partial}} = 0.006, p = 0.53$ ). The success of hypothesis 3 in the univariate analysis thus likely reflected the signal of greater resistance to dispersal from ocean as opposed to land, which was also captured in the depth surface, rather than an influence of ocean depth itself. Partial Mantel tests also strongly supported hypothesis 2 over hypothesis 1 (correlation between  $F_{ST}$  and resistance distance after controlling for geographic distance:  $r_{\text{partial}} = 0.69, p = 0.001$ ) but not the reverse (correlation between  $F_{ST}$  and geographic distance after controlling for resistance distance:  $r_{\text{partial}} = 0.02, p = 0.38$ ).

### **Genetic Variation on Islands**

There was a high correlation ( $>0.7$ ) between the straight-line and linkage estimates of distance from river mouth and the geographic and resistance distance estimates from the mainland. Straight-line distance to river mouth and geographic distance from mainland were thereafter excluded from analysis in favour of linkage distance to river mouth (distance to river) and resistance distance to mainland (distance to mainland). Akaike weights determined that the best multiple regression model for  $N_e$  included distance to mainland and distance to river (Table 1; AICc weight = 0.35).

The  $N_e$  increased as distance to river increased and decreased as distance from the mainland increased (regression coefficients and their standard errors, revealing the direction and strength, are plotted in Fig. 3). Distance to mainland was nearly twice as important as distance to river for  $N_e$  (Table 2). The best model for  $H_e$  included distance to mainland only (Table 1; AICc weight = 0.38);  $H_e$  was greater on islands closer to the mainland (Fig. 3b). Distance to river and distance to nearest island were included in the second and third top models for  $H_e$ , respectively. However, these terms did not increase the likelihood of the models (Table 1), and their confidence intervals included 0 (Fig. 3b).

Thus, only an effect of distance to mainland was supported. This was reinforced by the relative importance scores of the variables (Table 2).

Distance to river was included in the top model for  $N_e$ , suggesting that populations farther from a river mouth had a greater number of alleles (Table 2). However, the independent influence of this predictor was negligible and not strongly supported in the models (Fig. 3; Table 2). We suspect data points far from a river mouth yet close to the mainland influenced the relationship between genetic diversity and distance to river. Multiple regression was repeated without islands that were >80 km from a river mouth yet within 2 km of the mainland. With the exclusion of three islands, distance to river was not included in the top model for  $N_e$ .

## **Discussion**

### **Geographic Isolation**

Distance to mainland had the strongest effect on genetic variation within island populations, whereby islands farther from the mainland had lower levels of genetic variation than islands closer to the coastline. Similar results in herpetofauna have been observed within island and mainland populations by, for example, Sumner et al. (2004) and Hurston et al. (2009), although in these cases allelic richness (equivalent to  $N_e$ ) was the only measure of variation to correlate with any environmental variables related to insularity. This is often observed because heterozygosity ( $H_e$ ) can be less sensitive to bottleneck events than allelic diversity (Hurston et al. 2009). Our models with genetic diversity measures of  $N_e$  and  $H_e$  indicated that gene flow exists between mainland populations (high genetic diversity) and nearby island populations because they showed a strong relationship between island distance to mainland and high levels of genetic diversity. It is highly likely that instances may arise whereby an individual may disperse to these very near islands from the mainland, thereby offsetting the effects of genetic drift by introducing new alleles into the population (Clegg & Phillimore 2010). Purrungku Island, for example, is connected to the mainland at low tide, and six other islands are within 1 km of the mainland coast (Fig. 1).

The influence of isolation was further assessed using measures of population differentiation ( $F_{ST}$  and  $R_{ST}$ ), where it was found that the nature of the surrounding matrix (i.e., land versus ocean) had substantially more effect than geographic distance, per se, on the movement of individuals between populations. The absence of a strong correlation between genetic differentiation and geographical distance suggests a pattern associated with a lack of regional equilibrium and that genetic drift is much more influential in driving levels of genetic variation and differentiation than gene flow (Hutchison & Templeton 1999). This pattern (case-III in Hutchison and Templeton [1999]) has been observed for a number of species within similar island systems (e.g., Jordan & Snell 2008; Hurston et al. 2009; Hoeck et al. 2010). These studies credit this result to lowered dispersal ability over seawater and thus represent island systems where genetic differentiation and reduced variation occurs in the absence of gene flow between islands.

However, a test that uses only geographical distance assumes that the matrix through which individuals are dispersing is homogenous, although it may often consist of both land (i.e., other islands) and ocean. Therefore, it assumes that organisms are likely to follow the straight-line route between populations and that the geographic distance is an effective estimate of actual connectivity between habitats. In many landscapes this is inaccurate. The positive correlation between genetic differentiation and the model that included ocean as a barrier (hypothesis 2) indicated that populations were more similar when separated by shorter distances over water (Fig. 2), and this model more effectively captures this scenario. This model indicated that islands were more similar when connected by a chain of islands, which can be used as stepping stones to disperse from one island to another. These results suggest that the Kimberley island system is conducive to moderate levels of dispersal. Recent studies of the Kimberley Islands by Palmer et al. (2013) and Gibson (2014) suggest that reptile dispersal may be aided by the large tides and frequent high-rainfall events that occur in the region, coupled with abundant vegetation that could function as rafts. Islands that are more isolated by ocean are much less likely to encounter migrants and are more susceptible to the effects of genetic drift (Hutchison & Templeton 1999).

Isolation by bathymetry was measured to assess the impact of sea-level on dispersal ability. Given the islands were formed as a result of rising sea level approximately 8000 years ago, depth can be used as a proxy of time since isolation. Circuit theory has been used to examine the effects of sea level rise by, for example, Goulson et al. (2011), who showed that models with bathymetry (as a proxy for time since isolation) have a strong fit with genetic differentiation in a species with a low dispersal ability over water. In our study, which indicates that *C. inornatus* is capable of cross-ocean dispersal on a local scale, it appears that ocean depth is not strongly related to genetic differentiation in this species. Any legacies of historic land connections on population structure are likely to have been overwhelmed by the influence of more recent gene flow between islands.

### **Island size**

Island size was not a strong predictor of microsatellite diversity in this study and had the lowest relative importance of the island characteristics considered (Table 2). However, other studies show island size has a positive effect on genetic variation (e.g., Hinten et al. 2003; White & Searle 2007; Jordan & Snell 2008). Populations on large islands are likely to be larger and more able to retain greater levels of genetic variation. Island size may also influence dispersal and genetic differentiation by providing a larger target for dispersing individuals. Such effects were visually evident in the movement estimates (proxied by net current density) (Fig. 4) derived from connectivity modeling.

Where genetic drift is considered the primary driver of genetic population structure, island size has a comparatively stronger influence on levels of genetic variation than we observed (e.g., White & Searle 2007; Jordan & Snell 2008; Hurston et al. 2009). However, across the Kimberley islands, island size was less important in determining population structure. This indicates that even small islands, if well connected, may still maintain a sufficiently diverse population. Approximately 90% of the islands sampled were over 100 ha and therefore may not have been small enough to affect genetic variation within resident populations of *C. inornatus*.

## **Applying Connectivity Models to Conservation Planning**

For species persistence, effective conservation must protect the ecological and evolutionary processes that maintain genetic diversity. Our results exemplify the advantage of incorporating insights from isolation-by-resistance models when determining the drivers of population structure across a heterogeneous landscape. Moreover, models based on circuit theory have great applied value and may also be used for more illustrative purposes (Manel & Holderegger 2013). For example, the resistance models developed for *C. inornatus* have been used to map expected movement rates between islands in the Kimberley system (Fig. 4). In contrast to pairwise estimates of resistance distance, these maps represent the expected flux of migrants from the mainland en route to that or any other island. This form of information is highly compatible with landscape-scale conservation planning to prioritize islands for conservation and anticipate the movement of individuals from an identified source. Those islands with high predicted movement fluxes (high current density values) may be especially valuable for conservation because they are likely to support regionally high levels of genetic diversity and provide critically important linkages connecting island groups to the mainland. However, species perceive and respond to the landscape in different ways. Although *C. inornatus* is a useful model species to investigate connectivity across this system, robust conservation decisions should consider connectivity expectations across a range of species with different movement characteristics.

Conversely, it is also important to consider the potentially detrimental effects of connectivity to conservation goals. An island or island system that facilitates the dispersal of genes may also be more likely to facilitate the spread of pathogens, parasites, and invasive species (Storfer et al. 2010).

Continental islands are clearly important for maintaining biodiversity, and their value is further enhanced as model systems to explore the effects of insularity on fragmented populations. This study presents a valuable opportunity to compare previous studies with a much larger island system.

Distance to mainland and island connectivity appeared to have a large effect on the preservation of genetic diversity within insular populations of *C. inornatus* in the Kimberley region. Island size had relatively less effect on genetic variation than observed in other studies where genetic drift was considered to be dominant (White & Searle 2007; Jordan & Snell 2008; Hurston et al. 2009). Results



of studies such as ours may not only inform the management of island landscapes but also may inform the management of habitat on the mainland that has become fragmented due to anthropogenic activity. Furthermore, our findings highlight the importance of using complementary analyses to address the complexity of landscape-scale population structure. Using a combination of multiple linear regression, circuit theory, and distance matrix correlations gave a much clearer picture of the mechanisms in place over this landscape than each could have in isolation.

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Figure 1. Locations of islands off the coast of Australia sampled for *C. inornatus* that were analyzed for the present study (top left: CH, Champagne Island; JUN, Jungulu Island; AU, Augustus Island; UW, Uwins Island; SA, Saint Andrew Island; CORO, Coronation Island; KE, Keraudren Island; HE, Hedley Island; COL, Colbert Island; WO, Woodward Island; BON, Bonaparte Island; BOO, Boongaree Island; top right: NM, North Maret Island; SM, South Maret Island; BE, Berthier Island; BI, Bigge Island; WM, West Montalivet Island; EM, East Montalivet Island; DO, Don Island; UN, Unnamed Island; PU, Purrungku Island; CAP, Capstan Island; DE, Descartes Island; FE, Fenelon Island; LF, La Fontaine Island; CORN, Corneille Island; MO, Middle Osborn Island; SWO, South West Osborn Island; CAS, Cassini Island; bottom left: SU, Sunday Island; LO, Long Island; HI, Hidden Island; IR, Irvine Island; BA, Bathurst Island; KO, Koolan Island; NWM, North West Molema Island; KI, Kingfisher Island; WU, Wulalam Island; ST, Storr Island. SGM, Sir Graham Moore Island; AD, Adolphus Island).

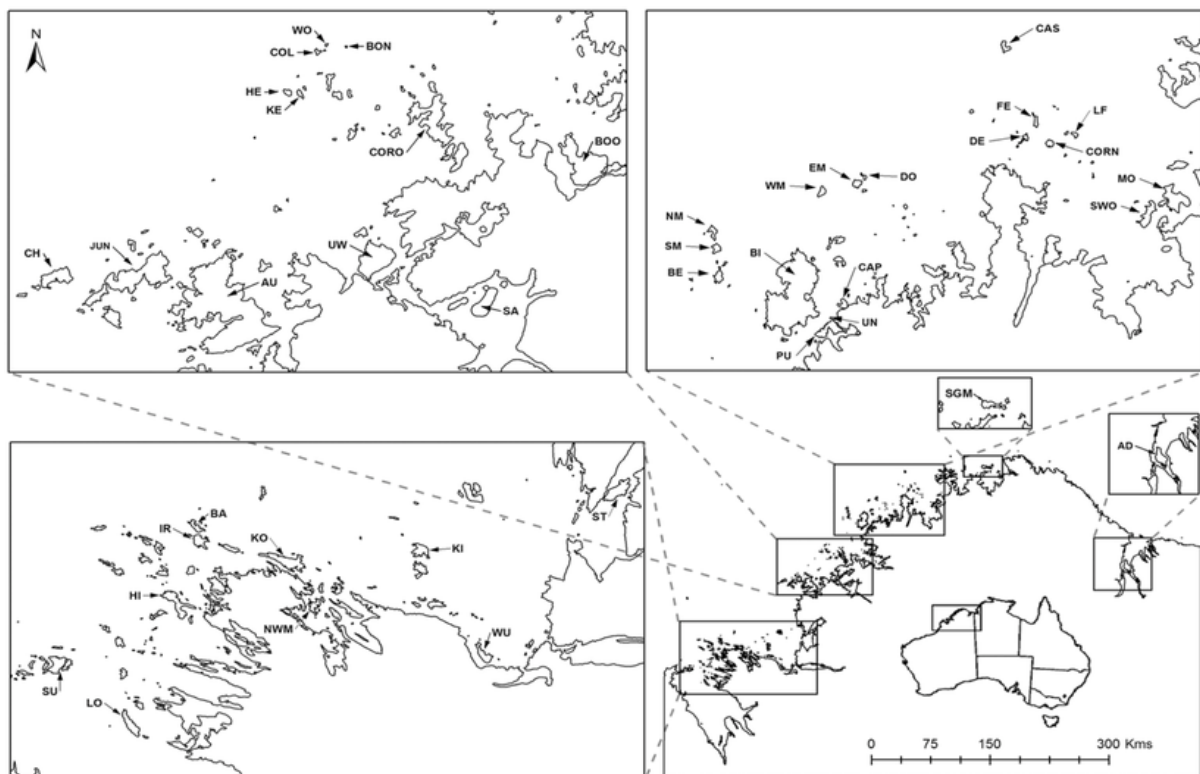


Figure 2. The relationships between pairwise genetic distance between populations of *C. inornatus* (estimated as  $F_{ST}$ ) from the Kimberley region of northern Australia and (a) geographic distance (hypothesis 1); (b) resistance distance (resist100.dist), where land resistance was weighted as 1 and ocean resistance as 100 (hypothesis 2); and (c) resistance distance, where land resistance = 1 and ocean resistance = ocean depth plus 10 (hypothesis 3) (see text for hypotheses). Trend lines, regression coefficients, and significance of the relationships are shown.

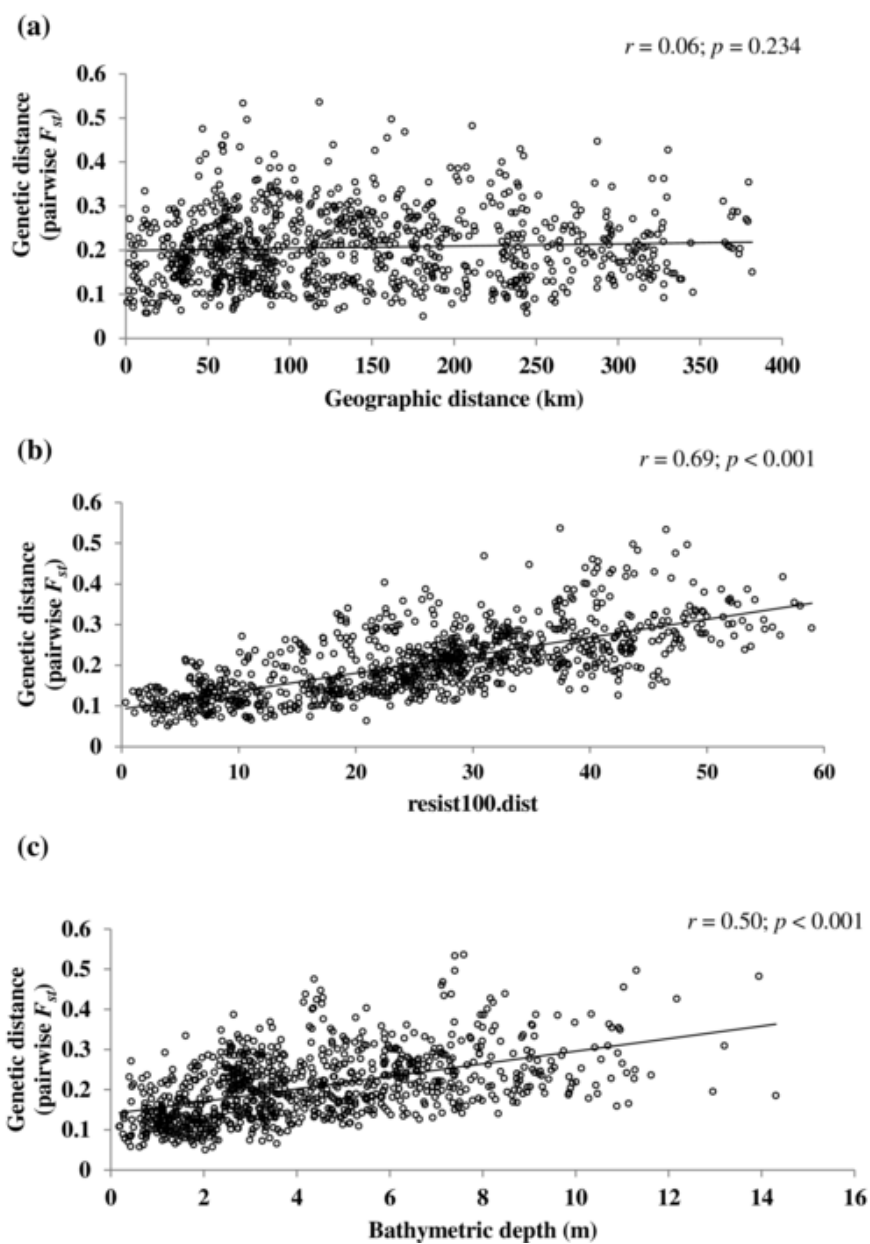


Figure 3. Effect size (regression coefficient) of explanatory variables on (a)  $N_e$  and (b)  $H_e$  of Kimberley island populations of *C. inornatus* for models with  $\Delta AIC$  (Akaike's information criterion) value  $\leq 2$  (Table 1) (bars, 95% CI; see Supporting Information for results of all regression models; DtoM, distance to mainland; DtoR, distance to river; DNI, log-transformed distance to nearest island). Model 1 is the top model for that response variable, followed by model 2 and model 3.

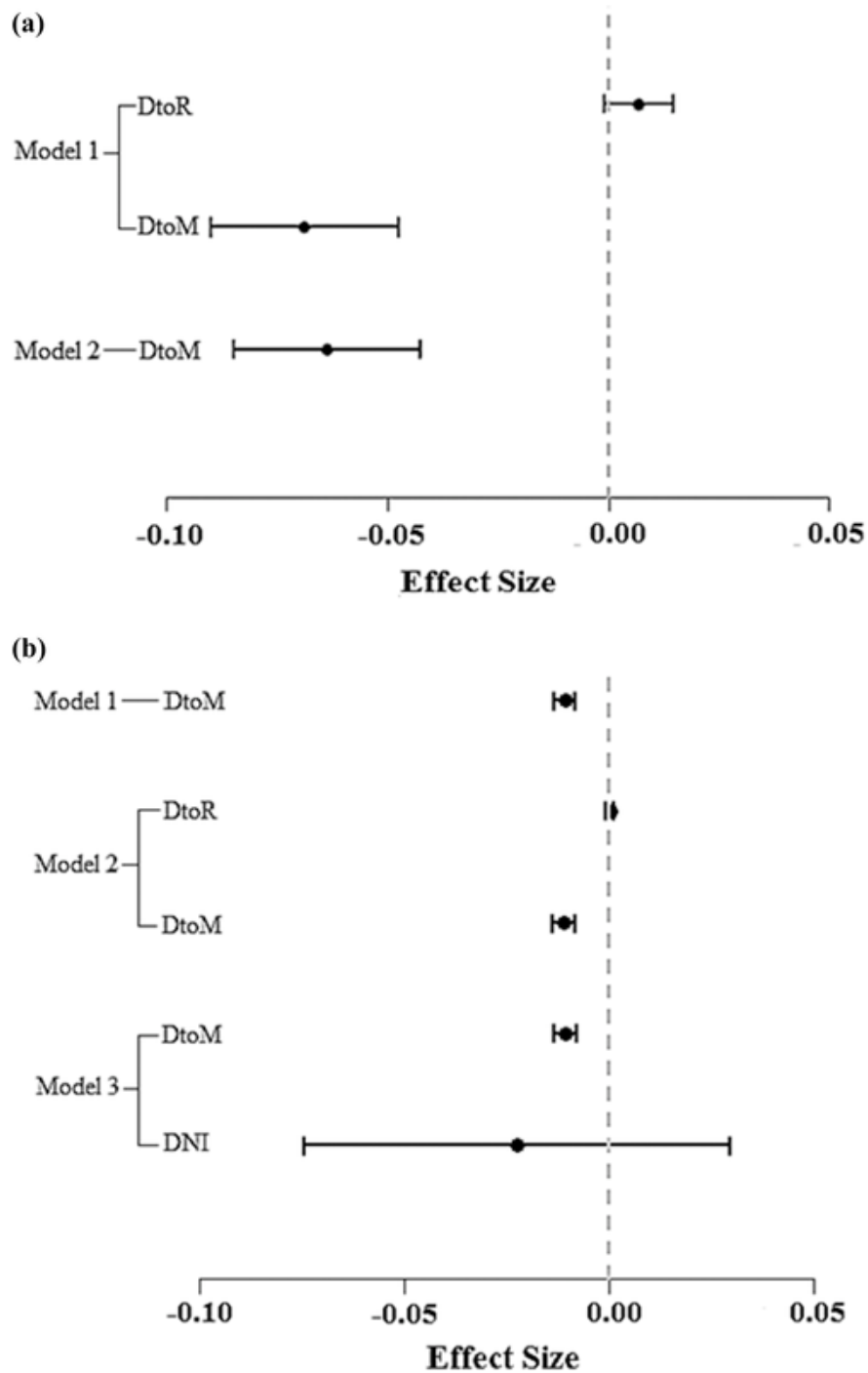


Figure 4. Circuitscape model of net current density, illustrating expected movement rates of *C. inornatus* from the mainland Kimberley (source) to all possible islands (destinations) under the resistance surface for hypothesis 2 (ocean as a barrier to dispersal, see text).

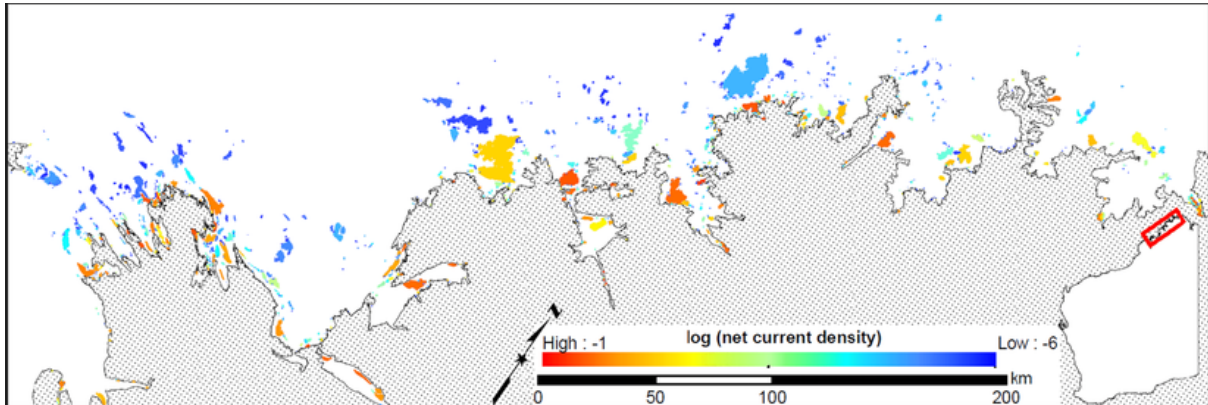




Table 1. Results of model selection and regression analysis of the genetic variation of island populations of *C. inornatus* in the Kimberley region of Western Australia modeled by physical island attributes.\*

<b>Model</b>	<b>AICc</b>	<b><math>\Delta</math>AICc</b>	<b>AICcWt</b>	<b>LL</b>
Effective number of alleles ( $N_E$ )				
DtoM + DtoR	84.48	0	0.35	-37.65
DtoM	85.4	0.92	0.22	-39.36
Expected heterozygosity ( $H_E$ )				
DtoM	-78.22	0	0.38	42.45
DtoM + DtoR	-76.70	1.52	0.18	42.94
DtoM + DNI	-76.55	1.67	0.16	42.86

\*Results shown for models with a  $\Delta$ AIC  $\leq$  2. Abbreviations: DtoM, distance to mainland; DtoR, distance to river; DNI, distance to nearest island (log transformed); AICc, Akaike's information criterion for small sample size; AICcWt, AICc weight; LL, log likelihood.

Table 2. Relative importance value of explanatory variables in models of genetic diversity of island populations of *C. inornatus* in the Kimberley region of Western Australia, based on the sum of Akaike weights of the models that include the variable

<b>Model</b>	<b>Explanatory variable</b>	<b>Relative importance value*</b>
Effective number of alleles ( $N_e$ )		
	distance to mainland	1
	distance to river	0.58
	distance to nearest island	0.25
	island size	0.25
Expected heterozygosity ( $H_e$ )		
	distance to mainland	1
	distance to river	0.3
	distance to nearest island	0.29
	island size	0.22

\*Values closer to 1.0 are of highest importance.